AN EVALUATION OF ANTHENANTIA (POACEAE)

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ABSTRACT

Anthenantia, a small Panicoid grass genus of the southeastern U.S.A. is evaluated morphologically. The two previously known taxa, A. rufa (Elliott) Schultes, and A. villosa (Michx) Beaux, together with a proposed new species. A. texana, are described, compared, and illustrated, and their relationships are discussed.

RESUMEN

Se evalúa morfológicamente Anthenantia, un pequeño género de graminea panicoide del sureste de Estados Unidos. Los dos taxa conocidos previamente, A. rufa (Elliott) Schultes, y A. villosa (Michx.) Beauv. junto con la nueva especie propuesta, A. texana, se describen, comparan, e ilustran, y se discuten sus relaciones.

Anthenantia Beauvois is treated in most recent floras (Small 1903 1933; Hitchcock 1951; Radford et al. 1968; Correll & Johnston 1970; Gould 1975; Hatch et al. 2001; Barkworth et al. 2003), as a panicoid grass genus of two species, these confined to the Coastal Plain Physiographic Province and adjacent physiography within the southeastern United States from eastern North Carolina to Florida, westward (exclusive of the Mississippi Embayment) to Arkansas and eastern Texas. The genus was named by Palisot de Beauvois (Ess. Agrost. 48, 151, pl. 10, 1.7, 1812) and based upon Phalaris villosa Michx. (Fl. Bor. Amer. 1:43. 1803). A second species, Aulaxanthus rufus Elliott (Bot. S.C. & Ga. 1:103. 1821), was incorporated by Schultes (Mantiss. 2:258. 1824), thus becoming A. rufa (Elliott) Schultes and forming a bitypic genus. So far as southeastern U.S.A. floristics are concerned, the only supplemental descriptive information appears to have come from G.V. Nash, who noted some extra-typical A. rufa in populations of that species from South Carolina westward, these mentioned in J.K. Small's Flora (1903, p. 79), as "A form, A. rufa scabra Nash."

Lately I have had some questions on the genus, the provocation being first from trying to fit the two previously known species into my "Guide to the Flora of Alabama and Middle Tennessee" (in prep.), second from trying to understand the patterns of morphological variation over the known range of the genus. Trips to and from Fort Worth, Texas across the Gulf South in recent years, together with fieldwork over much of the southeastern U.S.A. over the past four decades and study of collections in the herbaria BRIT/SMU. DUKE, MISSA, NO,

TAES, TENN, TEX/LL, and USF have allowed me to form concepts regarding these taxa. As a result, a third taxon has been discovered.

In this study the sequence will be 1) detailed discussion of Anthenantia as a genus, presented in standard descriptive sequence; 2) a descriptive key, including the new species; 3) technical descriptions of the three, each followed by some discussion of habitat and distribution; 4) illustrations, the first three being figures of the species, the fourth a plate with additional morphological detail.

Anthenantia Beauv, Ess. Agrost. 48, 151, pl. 10, f. 7. 1812. Type Species: A. villosa (Michx.) Beauv [- Phalaris villosa Michx.].

Habit loosely caespitose, slender perennials, perennating by shallow, concavelyarching, scaly rhizomes spreading as axillary branches from older shoot bases. Roots fibrous, shallow; adventitious roots not observed. Culms wandlike, mostly 70-120 cm tall, terete, finely multicostate, smooth, leafiest at and toward base. Leaves lowermost transitional to rhizomal scales, almost entirely multicostate, firm, scale, just upculm transitional to short, then longer, bladed members, then to uppermost ones, most distant and with long, tubular-conduplicate sheaths and short, erect blades; lower (basal) sheaths often open, either angled- or rounded-concave; upper sheaths progressively more rounded-conduplicate, tubular: leaf blades linear or lance-linear to linear-spathulate or linear-gladiate, flat to strongly involute or flattened-conduplicate, the margins variously hirsute or pilose-ciliate, scabro-ciliate, scaberulous, or entire, the apices mostly asymmetrically broadly acute, scabro-serrulate, often with midrib exsert as a mucronula; surfaces strongly multicostate, abaxially smooth, adaxially with strongest costae, these and their intervals smooth to variously scaberulous or papillate, sometimes with rounded microhairs, and in one species with erect. pilose intercostal hairs to 2 mm. Ligule present as a narrow, transverse, purplish or brownish, often sinuous zone, this elevated as a low erect to antrorse ridge or scale crested with minute to elongate papillae, ciliae, tubercles or scales. or erose. Note! Measures and character of ligules are taken from lower culm leaves; ligules of median and upper leaves can sometimes have longer hairs or scales than given here! Inflorescence paniculate, the upper scape a slender, naked peduncle above the short, erect blade of the elongate-sheathed upper leaf, mostly narrowly oblong to elliptic, lanceolate or ovate in outline, compact or loose, mostly 10-20 cm, the lowest nodes with primary branches whorled and usually longest, the internodes progressively closer, with progressively shorter primary branches, ultimate branching and rebranching sinuous, bending upward, terminating in cupuliform receptacles. Spikelets erect on cuplike receptacle, at maturity broadly obovoid or ellipsoid, slightly compressed dorsiventrally, 3-4 mm long, exposed surfaces greenish and/or reddish, and at maturity

densely cloaked with narrow, longitudinal bands of reddish, pinkish or pale. sharp, straight trichomes 1-2 mm long, lending a fuzzy look to the whole inflorescence; first glume lacking; second glume and lower lemma broadly obovate, oboyate or elliptic, cupuliform, slightly longer than all other spikelet parts. abruptly acuminate, 5-nerved with broad, hyaline, entire borders, the opposing lemma slightly narrower, less convex, both with strong bands of trichomes alternating with the median nerves, but the outermost (lateral) nerves narrowest, surmounted by waxy-papillose zones with protruding trichomes, the second glume with its thin border lapping over the edges of the opposing lemma. Lower (first) lemma and its palea sterile or male, rarely with a bisexual floret, the palea hyaline, oblong-oblong-ovate or oblong, mostly apically two-toothed. shallowly two-keeled, two-nerved, or nerves lacking, entire 'with broad involute borders. Second lemma and its palea enclosing a perfect flower, cartilaginous, narrowly ovoid or lance-ovoid, plano-convex, at maturity brown to deep red-brown or appearing nearly black, with hyaline borders broadening toward scale apex, those of lemma finely ciliate, both with acuminate, incurved, crisped-bordered tips, at anthesis looking like a slightly opened bird's beak, the lemma back strongly rounded proximally, the palea slightly rounded apically, medially and distally two-nerved, shallowly two-keeled, plane or slightly concave between the nerves. Florets those of the lowest (first) lemma either male or sterile; those of the upper (second) lemma bisexual. Perianth of two, asymmetrically flabellate, bilobed lodicules. Stamens 3, anthers oblong-linear to elliptic-linear, extrorse, 1.5-2.5 mm long, the very accrescent filaments attaching to anther adaxially at a very short connective, shoving the anthers out of the floret apex as they reach lengths of 4 mm or more. Ovary at anthesis with uneven dorsiventral symmetry, looking much like an ovoid-bodied, smallheaded insect, the arched abaxial and convex side with two short, broad, lateral grooves, the more level, adaxial side with a broad, shallow, concave surface, the small "head" with two lateral, narrowly subulate-terete branches, these bent outward, proximally, then upward, narrowing distally, ca. 2.5 mm long, each abruptly thickening to become the axis of a dark, dense stigmatic "brush" ca. 2.5 mm, these shoved out laterally as the floret opens. Carvopses broadly and tumidly obovoid, 1-1.8 mm long, yellow-brown, the bulbous apex apiculate, the oblique base dorsiventrally narrowed and oblique, the hilum an oblong depression on the palea side, the embryo under a large, rimmed disc on the lemma side.

Distribution.—Three species in North America, Atlantic and Gulf Coastal Plain and contiguous physiography exclusive of the Mississippi Embayment, North Carolina south to peninsular Florida, west to southern Arkansas and eastern Texas

Phenology.—Typically flowering from mid-July through October.

KEY TO THE SPECIES

1. Adaxial surface of leaf blade with erect or variously directed, strumose pilosity, these hars arising from intercostal sulcae; principal leaves with blades shallowly auricled, slightly bent outward from sheath; longer primary panicle branches 1/3–1/2 as long as whole panicle, these usually naked-based and widely ascending (to 45° or slightly more) giving panicle an ovate or broadly elliptic outline; glume and lower (outer) lemma surfaces often with longitudinal broad, reddish bands; spikelet trichomes commonly reddish, or pale with red or pink tips; ligule base reddish, its edge ascending ciliate the pale hairs to 1(-15) mm.

1. A. texana

- 1. Adaxial surface of leaf blade lacking trichomes of any sort (save for occasional papillae or microhars), sometimes scabrid; principal leaves with blades either strongly auricled and bent outward from their sheathes, or lacking auricles and erect to gradually bowed outward with no geniculation; longer primary branches of panicle either less than 1/3 panicle length or branching near base, seldom (save in a few extremes of no. 3) widely ascending, and generally with a narrower outline and a denser look; glume and lower lemma with or lacking red pigmented longitudinal bands; liquile base with edge ranging from papillate: tuberculate to variously ciliolate or ciliate or with a line of narrowly triangular scales.
 - 2. Principal (lower) leaves strongly auriculate at junction of blade and sheath, thus blades of lower culm leaves 'breaking' away from sheaths at narrow to wide angles, these same ciliate at least proximally, with spreading to ascending strumose-hirsute cilia; pigmentation of leaves, spikelets and their trichomes usually with little or any red; fertile lemma and palea lustrous brown; anthers at anthesis brown; liguie rim of lower principal leaves minutely eros or lacerate-ciliolate or with a line of irregular, flat based cilia mostly under 1 mm

2. A. villosa

2. Principal (lower, bladed) leaves weakly, if at all, auriculate at junction of blade and sheath, thus this zone, if viewed from side, usually showing but a slight polyection and a few pilose hairs, sometimes ascending-pilose-ciliate at blade base, or lacking hairs entirely; blades not perceptibly "breaking" away (geniculate) but flowing into their sheaths, suberect or slightly excurved; pigmentation of leaves, spikelets and their trichomes variously reddish or purplish, thus the foliage, scapes and spikelets darker; fertile lemma and palea similarly lustrous but a darker, redbrown to near black; anthers at anthesis dark brown; ligule rim of lower principal leaves nearly perpendicular, its edge commonly papilises - tubercular minutely ciliolate, finely erose, or with a line of short narrowly-triangular-based pale cilia

3. A. rufa

Anthenantia texana R. Kral, sp. nov. (Figs. 1, 4). U.S.A. TEXAS. HOUSTON CO: 2.5
mi Wo Kennard city limit by TX Hwy 7, in Sam Houston National Forest; sandy
clay loam of clearings in and edges of pine (Pinus taeda, P. echinata) and hardwood flats, 30 Sep 2002, R. Kral 92270 (HOLOTYPE VDB: ISOTYPES AUA, BM, BAYLU,
CLEMS. DOV, DUKE. FLAS, FSU, GH, ILLS, JSU, K, KANU, M, MICH, MO, MU, NCSC,
NLU, OSC. P, TEX, U, UAM, UNA, USCH, US, VPI, VSC. WILLI).

Planta perennis, gracilis, laxe caespitose, squami-rhizomatosa, (40-)50-100(-120) cm alta. Folia principalia vulgo suberecta vel leviter excurvata, 15-50 cm longa, leviter auriculata, leviter geniculata, ad basim culmortum approximate, sursum remota, liquida albocilitata, clitis (0.5-)1c15 mm longis, laminae foliorm adaxialiter strumoso-pilosae, pilis erectes vel ascendentibus, ad 2 mm longis. Squamae exteriores spicularium alterne longitudine rubrae et virides. Lemma et palea secunda coriacea, atrocastanca. Ambreze mattruae atroferrupineae, ca. 2 mm longae.

Perennial (45-)60-100(-120 cm high, loosely caespitose, the shoot bases connected by short (-7 cm) concavely arching, shallow scaly rhizomes 2-4 mm thick. Culms slender, wand-like, leafiest at and toward base, the lowermost leaves mere ribbed vellowish scales 5-15 mm, soon grading to bladed members. Principal leaves (15-)20-40(-60) cm, ascending, the longest with blades several times longer than their open but somewhat "V"-shaped or rounded sheaths., grading to the uppermost, this with its erect blade much shorter than its convolute-tubular slender sheath; sheath summit with two low but evident, usually cartilaginous, pilose-edged auricles, the transverse narrow, usually purple, ligular scale projecting forward at an angle, its edge a band of pale ciliae (5-)1(-1.5 mm; blade lance-linear to linear, mostly 4-7(-10) mm wide, base thickened at rounded auricle area, there often ascending-pilose, here breaking from the sheath, distally narrowing, often flattened or "v"-troughed to plane or variably deeply concave or almost conduplicate, abruptly narrowed to a broadly and obliquely angled apiculate tip, abaxial surfaces of sheath pale to green tinged with red, those of blades mostly deep green; adaxial surface of blades pilose with pale, erect or ascending, pustular-based trichomes to 2 mm arising from deep intercostal sulcae. Panicle outline ovate to elliptic or broadly lanceolate, 7-15(-20) cm, the lowest group most distant, the primary branches ascending, sometimes to 45° or slightly more, the longest of a whorl also naked-based and mostly 1/3-1/2 or more the total length of the panicle, the whole with secondary branching progressively more and shorter toward branch ends, giving the wide panicle base a much more open look. Spikelets turgidly obovoid or ellipsoid. 3-4 mm, at flowering time with longitudinal smooth zones of second glume and outer palea reddish alternating with green, the alternating rows of pustular-based trichomes red to pale pink or purple. First palea hyaline, 2-keeled, bifid, hairless, slightly shorter than the opposing lemma, tristaminate or stamens lacking. Second lemma and palea about equaling subtending second glume, a deep, lustrous red-brown or near black, the hyaline margins gradually widening, ciliolate, to a crisped, ciliate apical border; flower usually perfect simply pistillate. Caryopses 1.5-1.8 mm long.

Distribution.—Sands, sandy clay loam, sandy peat or silts of pine flatwoods, pine-oak barrens, bog edges, ditchbanks, clearings, Gulf Coastal Plain and contiguous physiography west of the Mississippi delta, southern Arkansas, Louisiana and eastern Texas.

Phenology.-Flowering mid-July through October.

PARATYPES, U.S.A. LOUISIANA: Beauregard Parish: by US 171, 2.8 mi N of Ragley & jet. US 190E (with A. villosa) 14 Oct 2001, R. Kral 91997 (TROY, VDB, VSC), ca. 17 mi W of DeRidder by US 190, 30 Sep 2002, R. Kral 93287 (BM, BAYLU, CONN, CTB, EKY, FSU, GH, JSU, KANU, KNK, MICH, MISSA, MO, MSC, MU, NCSC, NY, OSH, PH, RM, TENN, U, UNA, USCH, US, VDB, VPI, VSC, WAT, WILLI.

Specimens examined (cited by county, collector and collector's number): ARKANSAS: Bradley Co.: Sundell & McIntyre 2788 (VDB). Calhoun Co.: Sundell, Amason & Etheridge 7876 (BRIT); Orzell

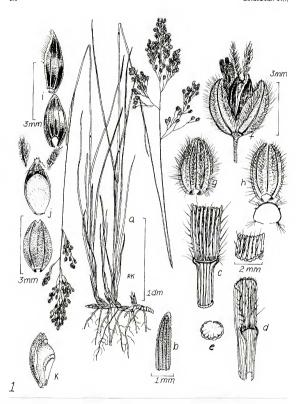


Fig. 1. Anthenantia texana (from the type, Kral 92270). A. Habit sketch. B. Leaf apex. C. Leaf sheath/blade junction, adaxial side (left), sector of leaf blade, adaxial side (right). D. Leaf sheath/blade junction, oblique view. E. Idealized cross-section of involute leaf blade. F. Spikelet at anthesis. G. Abaxial side of glume. H. Abaxial side of first (lower) lemma (above); idealized cross-section of same (below). J. Fruit, approaching maturity, two abcissed stigma brushes (above); abaxial side of fertile (upper) palea (below). K. Side view of fruit.

& Bridges 3058(SMU). Onachita Co.: Thomas & Doffitt 171881 & 669 (BRIT, NLU). LOUISIANA: Allen Parish: Shinners 22102 (SMU). Beauregard Parish: Shinners 21554 (NCSC, SMU). Grant Parish: Thomas, Barrett, Jones 1105 (VDB). Thomas et al. 12231, 12565 (VDB). Jefferson Davis Parish: Shinners 21469 (SMU). Natchitoches Parish: Bi.R. & H.M. MacRoberts 1202, 1550. MacRoberts 1198 (VDB). Thomas et al. 171,947 (BRIT). Winn Parish: Shinners 21940 (SMU). TEAAS: Angelina Co.: 13 Oct 1979. Fritz sn. (SMU). Aransas Co.: Blakey 45140 (TEN). Austin Co.: 15 Oct 1939. Tharp sn. (TFEN). Calloon Co.: 1 Dec 1928. Tharp, sn. (TAES, TEN). Freestone Co.: Kral 154 (SMU). Hardin Co.: Gould 11030 (SMU, VDB). Parks and Cory 19901 (TAES). Harris Co.: Frisher 10178. Houston Co.: Kral 932270 (VDB-Type). Jackson Co.: Silveus 340 (TEN). Liberty Co.: Gould 5419 (SMU, TAES). Newton Co.: Mahler 5199 with Weaver (SMU). Nucces Co.: Tharp 7918 (TEN). Robertson Co.: Lonard 2460 et al. (SMU). 2 Oct 1948. Parks sn. (TAES). Tew, Jr. 97 (TAES). Tyler Co.: Brown 3425 (TEN). Co. Tyler 27 (SMU).

This species has in the past been identified as A. villosa, particularly the broader and more distinctively auriculate-leaved, paler-haired examples (i.e. Texas specimens, Calhoun Co., 1 Dec 1928, B.C. Tharp [TEX]; Nueces Co., 25 Oct 1931, B.C. Tharp [TEX]). Many, because of their darker green or reddish pigmentation of foliage, darker spikelet pubescence, narrow, more erect leaves, have been identified as A. rufa (a large majority of east Texas examples, all Arkansas examples. most examples from western Louisiana. The "villosa" morphs of the species from southeast Texas may suggest a genetic influence of that species, since A. villosa is the only other Texas native, it and A. texana often mingling where ecotones are obliterated by disturbance. But, in such instances, the two appear to retain most, if not all, distinguishing features. In Beauregard Parish, western Louisiana, both west and east of DeRidder, I observed many hundreds of the two in recently logged areas of pine savanna. In each site A. villosa (Kral 91997B, 93286) occupied sandier small rises but often would be within a few feet of clumps of A. texana Kral 91997 A. 93287), which would be on slightly moister substrate. In those sites I had no trouble distinguishing the two, the former with broader leaf blades distinctly "breaking" away and with paler spikelets in narrower, denser inflorescences, the latter with narrower, geniculate, but less evidently so, and with darker spikelets in broader, more diffuse inflorescences. I plan further fieldwork in western Louisiana so as to see if there are examples there of mixed populations of A. texana and A. rufa and will prepare a report on that situation. Should there be such mixtures, from what information I have so far, all the A. rufa would be predicted to be forma scabra, while A. texana should show no scabrosity and a consistently geniculate leaf blade, together with a longer ligule. So, while there are distinct overlaps in regard to given characters for the three taxa, the pale, intercostal pilosity of strumose-based hairs is unique to A. texana

Anthenantia villosa (Michx.) Beauv, Ess. Agrost. 48, 151, t. 10, f.7. 1812. (Figs. 2, 4). BASIONYM: Phalaris villosa Michx, Fl. Bor. Amer. 1:43. 1803. Type: U.S.A. "In sabulosis Carolinae," Michx. Sn. (HOLOTYPE P).

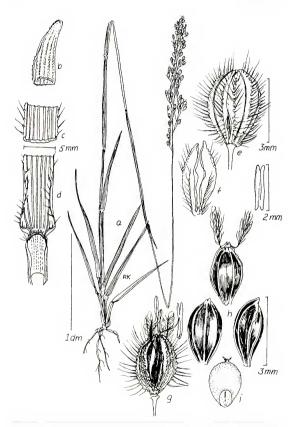


Fig. 2. Anthenantia villosa (Michx.) Beauv. (from Kral 90571). A. Habit sketch. B. Leaf apex, side view. C. Sector of lower leaf blade, adaxial viewed. Adaxial view of leaf/sheath junction. E. Side view of spikelet. F. An anomalous 'extra' floret (left); anther (right). G. Spikelet at anthesis. H. Three views of fertile (upper) floret, abaxial (palea side) view, stigma brushes protruding (above), abaxial view (below, left); side view (below, right). I. Mature caryopsis (Hillum side).

Aulaxanthus ciliatus Elliott, Sketch Bot. S. Carolina 1:102. 1816. Aulaxia ciliata (Elliott) Nutt., Gen. Pl. 1:47. 1818. Type: 'in dry pine barrens, flowers September - October,' (101.0TYPE: CHARL: PR. 3:057.)

Elliott suggested the possibility that his A. ciliatus might be the same as Phalaris villosus Mich. Lp. 43." To be sure of Elliott's concepts, I visited the Charleston Museum in December 2003 to examine the type material. Thanks to the consideration of Albert Sanders, curator of the Elliott Herbarium, I was quickly shown the Elliott types of Aulaxanthus ciliatus and Aulaxanthus rufus, both mounted on a single sheet and in good shape. The right hand specimen is a small but readily identifiable specimen (CHARL: "BY-3965") of Anthenantia villosa, marked by Weatherby as the type of Aulaxanthus ciliatus Elliott by Weatherby in 1941. To be absolutely sure of the identity of Michaux's Phalaris villosa, At my request, Barney Lipscomb (BRIT) made photocopies of my plates of A. villosa and A. rufa and sent them unlabelled to Porter Lowry (P). The Michaux type clearly matched my unlabelled plate of Anthenantia villosa.

Panicum erianthum Poir, Encycl. Sup. 4:284. 1816.

Panicum hirticalycinum Bosc. ex Roemer & Schultes, Syst. Veg. 2:468. 1817.

Perennial (50-)60-130 cm high, loosely caespitose, perennating by short, scaly rhizomes from older shoot bases, Culms slender, wand-like, leafiest at or toward base. Lowest leaves imbricate, yellowish, multicostate scales, grading to long-bladed principal leaves 15-40 cm, the sheaths rounded-conduplicate, opening distally, there with a narrow, wavy-transverse ligule, each edge terminating at a prominent thickened auricle, there with a tuft of pilose hairs, the ligule base ascending at a wide angle from the leaf surface, or even an erect, low wall of tissue, its edge variously short-ciliate (mostly not over 0.5 mm), or irregularly papillate-erose or with short, narrowly triangular squamellae; blades mostly lance-linear, lower ones distinctly breaking away from sheaths at various angles sometimes nearly 90°, 4-9(-15) mm wide, plane or inrolled, margins strumose-hirsute-ciliate, of ten also strongly papillose at least proximally, apex flat, triquetrous to rounded-conduplicate, or compressed-conduplicate, usually obliquely acute, scabro-ciliolate. Upper culm exserted 1-2 dm above the-erect, short-linear upper leaf blade as a slender peduncle terminating at a mostly narrowly elliptic to cylindric or lanceoloid panicle, this (5-)10-20(-25) cm, the whorls of primary branches ascending to erect, mostly closely rebranching to produce a generally dense, rarely interrupted inflorescence of yellowish to silvery-green spikelets. Spikelets oboyoid to ellipsoid, 3-4 mm long, the rows of pustular-based trichomes typically silvery or pale, the outer scales with mostly green or pale green surfaces, the hyaline first palea slightly shorter than its lemma, often with a line of ascending clear trichomes lateral to each keel, the floret either sterile or staminate: second lemma and palea coriaceous with distal edges hyaline-ciliate, surface brown to dark brown, this floret typically perfect. Anthers at maturity narrowly oblong-linear, ca. 2.5 mm, yellowish-brown. Fruit ca. 2 mm long, yellow-brown.

Distribution.—Sands, sandy clay, sandy loams, moist to rather dry sites, mainly pinelands, particularly the longleaf pine-turkey oak system, oak-pine

barrens and flatwoods, upper edges of bogs, ditchbanks, sandy clearings, Atlantic and Gulf Coastal Plain and contiguous physiography from North Carolina south to South Florida and west, except for the Mississippi Embayment, into eastern Texas

Phenology.—Flowering mid-July through October (or November in southern range).

Specimens examined: ALABAMA. Autauga Co.: Kral 33566 (VDB); Harper 4464 (UNA, VDB); McDaniel 7002 (MISSA, VDB). Baldwin Co.: Kral 29795 (VDB): Kral 29847 (SMU, VDB): Pennell 4551 (DUKE): Shinners 28901 (SMU), Tracy 8025 (TAES). Barbour Co.: Kral 28004 (SMU, VDB) Bibb Co.: Kral 52265 & 69548 Choctaw Co.: Kral 67840, Conceuh Co.: Kral 40972 (BRIT VDB), Covington Co.: Kral 33668 38107, 36804, 33688, 44692 (VDB). Crenshaw Co.: Kral 21993, 33722 (VDB). Escambia Co.: Kral 32477. 33873 (VDB). Geneva Co.: MacDonald 12225 (VDB). Houston Co.: MacDonald 3030 (VDB) Mobile Co.: Kral 29701 (VDB), 29717 (SMU, VDB); Silveus 1021 (BRIT, TEX). Monroe Co.: Kral 69707, 85370 (VDB). Russell Co.: Kral 44210 (VDB). Washington Co.: Kral 37263 (VDB); McDaniel 9913 (VDB). FLORIDA. Calhoun Co.: Godfrey 55581 (FSU, NCU, VDB), Godfrey & Kral 54160 (DUKE). Duval Co.: Curtiss 6258 (NCU). Escambia Co.: Silveus 5622 (TEX). Franklin Co.: Godfrey (FSU, VDB), Gadsden Co.: Godfrey 53585 (DUKE, FSU). Hernando Co.: Ray 9484 (FSU, USF, VDB). Hillsboro Co.: Lakela 23376 (USF), 25374 (SMU, USF, VDB). Jackson Go.: Godfrey 54264 (FSU), 54383 (DUKE, FSU, USF, VDB); Tacy 3850 (TAES) Leon Co.: Clewell 793 (VDB), Godfrey 56111 (FSU, USF, VDB); Kral 1789 (FSU, SMU, NCSG). Reese 640 (NCU) Levy Co.; Kral 15269 (VDB). Liberty Co.: Thorne & Davidson 16834 possible hybrid! (FSU). Madison Co.: Kral 6178 (FSU, VDB). Okaloosa Co.: Godfrey 57669 (FSU): 27 Sep 1950, West s.n. Santa Rosa Co.: Ford 5375 (NCU), Godfrey & Houk 62551 (SMU, VDB), Wakulla Co.: Kurz 169 (FSU). Walton Co.: Godfrey 57630 (FSU): Tyson 358 (USF). Washington Co.: Godfrey 55238 (FSU, NCSC). GEORGIA. Baker Co.: Thorne 6416 (Emory U.). Bryan Co.: Eyles 6814 (Emory U.) Charlton Co.: Kral 64651 (VDB): Jones 7290 with Carter (VDB, VSC). Early Co.: Kral 90344 (VDB). Thorne 6628 (Emory U.). Emanuel Co.: Kral 85477 (VDB); Wilbur 2910 (FSU, NCSC, SMU) Taylor Co.: D.S. & H. Correll 8401 (DUKE); Kral 85477 (VDB). Ware Co.: Silveus 5370A (TEX). LOUISIANA. Beauregard Parish: Shinners 22218 (NCSC, SMU, TEX), Kral 91997B (VDB); Kral 92286 (VDB), Grant Parish: Thomas et al. 3062 (VDB), 12565 (BRIT). LaSalle Parish: Laird 1069 (BRIT). Natchitoches Parish: Kral 16207 (VDB). Rapides Parish: Duncan 56031 (SMU, TAES, TEX), and 56041 (SMU, TAES). St. Tammany Parish: Bro. Arsene et al. 11251 (SMU). Vernon Parish: Thomas & DePoe 273 (VDB). Kral 93319 (VDB). Washington Parish: Allen 8684 (VDB). MISSISSIPPI. Forrest Co.: K.E. & L. Rogers 42011 (SMU); Weddle s.n. 9/10/40 (MISSA). Greene Co.: Rogers 1747-A (SMU Harrison Co.: Tracy 38+8 (NCU, TAES). Jackson Co.: A.B & A.C Seymour 178 (DUKE, NCU); 3 Aug 1889, Earle s.n. (DUKE); Weaver & Rushing 0186 (VDB), Jones Co.: Morgan 1439 (VDB), Lauderdale Co.: McDaniel & Clarke 14601 (VDB). Pearl River Co.: Jones & Sargent 13694 (VDB), 8432 (SMU); Reed 53 (FSU). Stone Co.: Shinners 28826 (SMU). NORTH CAROLINA. Bladen Co.: Blomquist 13622 (DUKE) Brunswick Co.; Blomquist 439 (FSU, NCSC). Cumberland Co.: Carter 2974 (VDB); Ahles & Leisner 33466 (NCU) Columbus Co.: Blomquist 14785 (DUKE). Duplin Co.: Ahles 33183 with Leisner (NCU, VDB). Harnett Co.: Godfrey 5685 (DUKE); Radford 8758 (NCU), Hoke Co.: Kral et al. 82990 (VDB); Ahles 36383 (NCU), Johnston Co.: Radford 29292 (NCU, SMU). Moore Co.: 10 Apr 1931, Blomquist s.n. (DUKE). Richmond Co.: Correll 7139 (DUKE). Radford 19232 (NCU). Scotland Co.: Ahles with Leisner 32863 (NCU). SOUTH CAROLINA. Allendale Co.: Ahles with Bell 18423 (NCU). Bamberg Co.: Ahles 37657 (NCU). Barnwell Co.: Batson, s.n. 27 Oct 1953 (NCU, USCH) Calhoun Co.: Ahles 35363 (NCU, VDB). Chesterfield Co.: Godfrey 8086 (DUKE): Radford 18646 (NCU). Colleton Co.: Ahles with Bell 15431 (DUKE, NCU). Darlington Co.: 22 Aug 1908. Coker s.n. (NCU). Edgefield Co.: Radford 30195 (NCU) Georgetown Co.: Godfrey 8109 (DUKE). Kershaw Co.: Radford 29984 (NCU). Lee Co.: Radford 29340 (NCU). Lexington Co.: Radford 29856 (NCU). Marion Co.: Bell 11012 (NCU). Orangeburg Co.: Ahles 35131 (NCU). Richland Co.: Godfrey 50758 (DUKE.

NCSC), Sumter Co.: Freeman 57880 (NCU), TEXAS. Hardin Co.: Parks & Cory 11145, 19900, 19902, 19903 (TAES), Japen Co.: Correll 38164 (SMU), 22 Aug 1941, Tharp s.n. (TAES), Newton Co.: 16 Sep 1947, Law sn. (TEX), Cory 49807 (SMU).

I have not yet seen the three *Anthenantia* in one place, although this might be possible in western Louisiana or even eastern Texas. But were such to happen, *A. villosa* would be distinguishable at a glance. It is the most robust of the three, has the least rusty pigmentation in leaf and culm (save sometimes for pinkish internodes and spikelet hairs), has generally paler vesture, the plants therefore giving the overall effect of pale green. The lower culm leaves are more visibly auriculate and tend to spread more, and the blade margins are more coarsely and conspicuously strumose-hirsute-ciliate. Pigmentation of anthers and of the coriaceous lemma and palea is paler. The hyaline palea of the lower (first) floret is unique, since it usually has rows of ascending, long, stiff, pale trichomes parallelling and external to each of the two keels (see fig. 4). On the other hand, in character of culm, in pigmentation, character and orientation of leaves and in character, shape, and indumentum of inflorescence, it is easy to see why the other two have traveled under the same epithet for such a long time. This will be discussed under *A. rufa*.

Anthenantia villosa occupies the driest habitats of the three. It extends further up sides of sandhills, is in higher zones within ecotones between uplands and low, and is in the higher spots in flatwoods and savannas. It is the most frequent associate of Aristida stricta in Longleaf pine sandhills. Future studies probably will show that there is genetic exchange between it and A. rufa and A. texana, particularly where ecotones have been broadened through disturbance.

3. Anthenantia rufa (Elliott) Schultes, Mant. 2:258. 1824. (Figs. 3, 4). BASIONYM Aulaxanthus rufus Elliott, Sketch bot. S. Carolina E103. 1816. Aulaxia rufa (Elliott) Nutt., Gen. Pl. 1:47. 1818. Panicum rufum (Elliott) Kunth, Revis. Gramin. 1:35. Monachne rufa (Elliott) Bertolini, Mem. Reale Accad. Sci. Inst. Bologna 2:596, t. 41, f. 1. 1850. Type: [SOUTH CAROLINA]* in savannas, and damp soils in the pine barrens, midway between Saltcatcher bridge and Murphy's on the Edisto," Elliott 523 (number assigned by Muhlenberg) (HOLOTYPE: CHARLI).

Leptocoryphium drummondii Müll, Berol., Bot. Zeitung (Berlin) 19:314. 1861. Type: U.S.A. LOUISI-ANA: [1831–1832?] T. Drummond.

Perennial (50-)60-125 cm high, loosely caespitose, perennating by short, scaly rhizomes from older shoot bases. Culms slender, wand-like, leafiest at or toward base. Lowest leaves mere scales, transitional to principal leaves 12-60 cm, with blades much longer than sheath; sheaths often red-brown or purpletinged, variously folded conduplicately, narrowing gradually to similarly folded blade, the connecting auricle minute or not evident save as a few pilose spreading hairs at ligule ends or even these lacking; ligule wavy-transverse, usually a narrow, erect ridge 0.2-0.4 mm high, typically purplish, its upper edge papillate, minutely lacerate, rarely ciliolate with cilia at most 0.5 mm (uppermost leaves

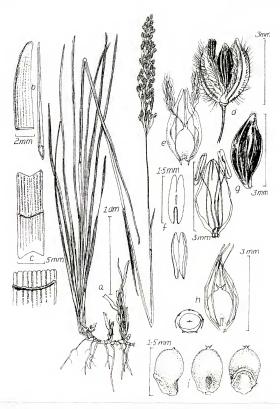
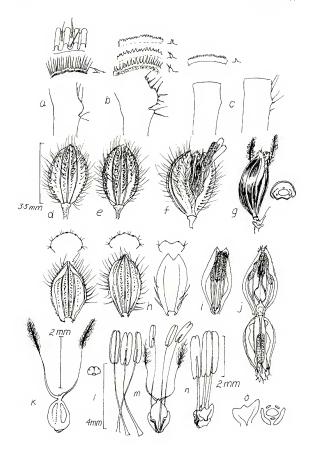


Fig. 3. Anthenantia rufu (EII.) Schult. (from Knd 19619). A Habit sketch. B. leaf apex, side view (left), adaxial edge (right). C. Leaf blade/sheath junction, lower leaf, adaxial view (above); leaf blade/sheath junction, adaxial view, ligule. D. Spikelet at anthesis. E. "Cleared" fertile lemma with young developing fruit. F. Adaxial view of anther. G. Adaxial view of first (lower) palea at anthesis (below left); side view of upper (second) lemma and palea (above right). H. Perfect floret, with ripening fruit (right); idealized cross-section of perfect floret, including lemma (left). I. Three views of ripe fruit, side view (left), hilum side (middle), embryo side (right).

often with distinctly longer cilia!); blades mostly erect to ascending-excurved, continuous with sheath apex, not at all geniculate, linear to linear-gladiate or linear-spathulate, (3-)4-8(-10) mm wide, flat to rounded-involute or variously folded-conduplicate, margins entire,- or sparsely pilose-ciliate proximally, or scabrid, the surfaces pale to deep green, or purple-tinged, smooth to papillate or scaberulous on the costae, apex mostly conduplicately sharply folded, or open at a wide angle, obliquely broadly acute, apiculate. Panicles ovoid to lanceoloid. ellipsoid, or cylindric, (8-)10-20(-25) cm, branching mostly strongly ascending to nearly erect, the lowest whorl often with some primary branches 1/3 the total panicle length or more, but mostly floriferous to near base, thus the inflorescence mostly dense. Spikelets mostly broadly ellipsoid to obovoid, 3-4 mm, with exposed outer surfaces alternating with longitudinal bands of green and red, the bands of trichomes reddish to deep purple, rarely pinkish, very rarely pale. Lower floret usually staminate, often sterile, sometimes perfect; upper floret with coriaceous lemma and palea deep red-brown or castaneous, appearing nearly black, the hyaline borders broadening distally, there ciliate, often crisped and finely ciliate apically, their flower usually perfect. Anthers at anthesis narrowly oblong, ca. 2-2.5 mm, deep purple-brown, appearing black. Ripe caryopses 1.5-2 mm, yellowish-brown.

Distribution.—Sands, sandy peats, silts and sandy clay of pine flatwoods and bogs, edges of bogs, acidic seeps and seep slopes, and pine savanna, Coastal Plain and contiguous geology, North Carolina south to peninsular Florida, west into Louisiana, possibly eastern Texas.

Specimens examined.—Note! In Small's Flora of the Southcastern United States (1903, p. 97) appears the citation., under Anthenantia rufa "A form, A. rufa scabra Nash, differing from the above in having the sheaths and blades scabrous, occurs in similar situations in South Carolina, but mainly from Alabama to Louisiana. Fall." This information appears in some present-day reference sources, but inconsistently, sometimes the taxon being given as a variety, in other instances as a "form" (as per Small). Since Nash and Small were colleagues at the New York Botanical Garden, and since Small passed along the characteristics in 1903 for what he referred to as a form, it must be assumed that the name received no further published attention. I have been unable to find any actual formal presentation, and Small appears to have let the matter lapse as of 1903; certainly it did not carry forward to his 1933 "Manual." Whatever the case. Nash should be credited for his observations. It is true that there are populations of scabrid A. rufa from the Carolinas west to Louisiana, and there are associated characters such as the presence (usually) of a tuft of pilose hairs at a small triangular projection where ligule meets margin, this often accompanied by a short line of slender pilose cilia above and below along contiguous margin. However, these latter characters tend to vary independently, as does the degree of scabrosity of leaf blades and sheaths. My own conclusion is



to leave the situation as Small had it. "Scabra" morphs show a gradation westward, particularly in the increase of scabrosity and hairs at and around the ligular edge, mostly from Alabama and panhandle Florida west into 'Louisiana. Regrettably, large loans from DUKE and NCU were annotated A. rufa without checking "scabra" characters. They are entered with an asterisk so as to provide an idea of distribution of A. rufa in the Carolinas, and a more careful check for the few, if any, "scabra" morphs will be made.

Anthenantia rufa (Elliott) Schultes forma rufa

ALABAMA. Baldwin Co.: Kral 79274 (VDB). Butler Co.: Kral 62998 (VDB). Conceub Co.: Kral 83306 (VDB). Kral 52367 (VDB). Geneva Co.: McDaniel 7958 (VDB); Kral 52367 (VDB). Houston Co.: MacDonald 1801 (VDB); MacDonald 3666 (VDB). Mobile Co.: John & Connie Taylor 15260 (BRIT). FLORIDA. no county but suspect Duval, 1883, AH Curtiss(TAES). Bay Co.: Kral 52190 (VDB); Codfrey & Houk 61532 (SMU). Gadsden Co.: Kral 644568 (VDB). Liberty Co.: Godfrey 84413 (BRIT, FSU). Wakulla Co.: Henderson 63-1379 (SMU). Walton Co.: Ward 7417 with Hunter (VDB). Washington Co.: Kral with Godfrey 5976 (DUKE, FSU). VDB). GEORGIA. Baker Co.: Kral 56732 (VDB). Coffee Co.: Kral 8766 (VDB). Long Co.: Kral 8864 (VDB). Pierce Co.: Kral 79975 (VDB). Turner Co.: Kral with Carter 8417 (VDB). Wayne Co.: Duncan 7670 (SMU). Worth Co.: Kral 81802 (VDB). LOUISIANA. St. Tammany Parish: 17 Nov 1936, Penfound sn. (NO). MISSISSIPPL. Hancock Co.: Clarke 5890 (BRIT). Harrison Co.: Tracy 3819 & 8590 (TAES). Jackson Co.: Tracy 82 (TAES). Earle 239A. NORTH CAROLINA. Bladen Co.: Ahles with Leisner 33368; Ahles 37599* (NCU). Brunswick Co.: Blomquist 1075, 10076 (TEX), Ahles 36235 (NCU). 5-MU). SOUTH CAROLINA. Bamberg Co.: Ahles 37755 (NCU). Chesterfeld Co.: Radford 18760* (NCU). Georgetown Co.: Radford 31389* (NCU).

Anthenantia-rufa (Elliott) Schultes forma scabra Nash

ALABAMA. Baldwin Co.: Wilhelm 1188 (VDB), Kral 78172, 89038 (VDB) Covington Co.: Duncan et al. 14181 (SMU); Kral 41655, 80081D, 86880 (VDB), Escambia Co.: Kral 13829, 44787, 44885 (VDB), Geneva Co.: Kral 90294 (VDB). Mobile Co.: Kral 26949, 93368 (VDB), Monroe Co.: Kral 44380, 69624, 90519. 90572 (VDB). Washington Co.: LeLong 6818 (VDB), Kral 25901, 90526, 90527 (this last one first identified as A. villosa because of pale spikelets, a large set to be distributed. (VDB). FLORIDA. Alachua Co.: Silveus 6742 (TEX). Baker Co.: Godfrey 74696 (VDB). Bay Co.: 2+ Oct 1980, Athey s.n. (VDB) GEORGIA. Tift Co.: Shepherd 237 (TAES). Ware Co.: Silveus 53+5 (TEX). Worth Co.: Kral 51569 (VDB). LOUISIANA, St. Tammany Parish: 17 Nov 1938, Penfound s.n. (NO) Vernon Parish: Thomas & Allen

Fis. A. Idealized sketches of floral and vegetative parts, Anthenantia. A. A. texana lower leaf, small sector adaxial side of blade (above); sector of ligule, adaxial side of leaf (middle); side view of leaf sheath/blade junction, showing trichomes at blade base and on auricle. B. Three ligular types, idealized for A. villosa, with three cross-sections (top); side view of leaf/sheath junction, A. villosa (below). C. A. rufa, lower leaf, sector of ligule and cross-section at right (above), side view of leaf/sheath junction, A. rufa forma rufa (below left) and forma scabar; (below right). B. A. texana glume, abaxial side (top), cross-section (middle; dots for nerves, lines for hairs); adaxial view (bottom). E. Opposing lemma, abaxial side (top); cross-sectional ideogram (middle); adaxial side (bottom). F. Side view of A. rufa spikelet, lower (staminate) flower at anthesis. G. Side view of A. rufa 'spikelet, lower (staminate) flower at anthesis. G. Side view of A. rufa 'spikelet, lower) palea, A. villosa (below), ideogram of cross section of same. I. Adaxia view, A. texana staminate flower and its palea just prior to anthesis. J. A cleared second (upper) floret of A. rufa opened 80 degrees, the perfect flower just prior to anthesis. K. Idealized view of young yoncocium, abaxial side. L. Three A. rufa stamens at anthesis. M. Perfect floret, Anthenantio. N. Side view of lower (staminate) flower, A. villosa, just prior to anthesis. O. Side view of lodicule, A. texana showing the typical nervation (left); ideogram of position of flower parts, the two lodicules, the three stames and the ovary at center.

98029 (N.L.U. VDB), Thomas 5568 (VDB), Washington Parish: Kraf 83043 (VDB) MISSISSIPPI, Hancock Co.: Jones 20345 (VDB); Sørgent 9307 (SMU); Clarke 5887 (BRIT) Harrison Co.: Tracy 3819 (TAES). Stone Co.: Kraf 93351 (VDB), NORTII CAROLINA, Hitchcock 290 (LL).

CONCLUSIONS

My study of Anthenantia has been based on field observation along with careful artwork and morphologic evaluation. Such foci allow the following:

1. Anthenantia, so far as the North American flora is considered, is a distinct genus of panicoid grasses. It is the only genus in our area to combine (1) a scaly-rhizomatous, loosely caespitose habit (2) a paniculate inflorescence, with (3) spikelets similar to those of Panicum but lacking a first glume, (4) the second glume and first lemma 5-nerved, with at least the median three flanked by narrow longitudinal rows of elongate, often papillose-base (strumose) trichomes, and (5) two florets, the lower "glumclike" lemma with its hyaline, bicarinate palea enclosing a male floret or sterile, the second (or upper) lemma and palea coriaceous, enclosing a (usually) perfect floret.

2. A third "species-level" taxon, *Anthenantia texana*, exists west of the Mississippi Embayment, where it may share area, if not exact habitat, with *A. villosa* and possibly also *A. rufa* in eastern Texas and western Louisiana. *Anthenantia texana* may actually be the only species to be found in Arkansas.

3. An examination of the synonymy and taxonomic dispositions in Anthenantia and morphologically adjacent genera seems (to me) to show a definitely confused set of concepts. Since the whole tribe, for that matter the whole family, is having a vigorous and very controversial "shakedown," it is useful to point out two genera with strong resemblance to Anthenantia, namely Leptocoryphium Nees and Melinis P. Beauv. Leptocoryphium has two species: L. lanatum (Kunth) Nees ranges from Argentina north into Mexico and the Anti'lles, in the north of its range frequenting pine savanna, oak-pine land, open savanna, and pasturage within these systems. In short, it has an "Anthenantia-type" habitat. My first encounter with the species was in Nicaragua ("Zeylaya, burnt savanna by road to Limbaika, ca. 1 km e of jct. rd to Limbaika, 10 July 1982, R. Kral 64344"). I did not identify the plant but did note its strong resemblance to Anthenantia. From my recent examination of herbarium material and from excellent descriptions by Pohl for Flora Meso-america (1994) and Flora Nicaragua (2001), I am further intrigued. The species is described as having a cormose, fibrillose base but otherwise seems to differ vegetatively from Anthenantia in no significant way. The inflorescence is paniculate, sinuously branched, the spikelets are similar in design, the lower glume is lacking, the second glume and lower palea have the same nervation, with trichomes elongate and in longitudinal rows. The only significantly different character state in the spikelet seems to be in the lower floret, which has no palea and which is sterile. The upper floret in character and dimensions of lemma and palea and in perianth, stamens, and

gynoecium is very similar. The fruits are similar. I suggest that if a tight description of *Leptocoryphium* were spaced so that a similar one of *Anthenantia* were laid in on alternate lines, there would be a strong agreement. It is significant that one of the most excellent of observers, George Bentham, treated *L. lanatum* as *Anthenantia lanata* (Kunth) Benth.

Melinis P. Beauv., an African genus of 22 species, also is similar to Anthenantia but appears to be a more distant relative and is in fact placed in subtribe Melinidinae by current authors, while Anthenantia and Leptocoryphium are morphologically aligned with subtribe Digitariinae. The two species of Melinis in the Americas are the weedy invasives M. repens (Willd.) Zizka ssp. repens (Rhyncheletrum repens [Willd.] C.E. Hubb. = R. roseum (Nees) Stapf & C.E. Hubb.) and M. minutiflora P. Beauv, which are rapidly occupying disturbed sandy or gravelly areas (overfarmed situations, fields, railroad rightsof-way, etc.). The former has gotten into the range (if not the habitat) of Anthenantia in northern Florida, south Georgia, and Texas. The latter is so far confined to Florida. A quick scan of a living M. repens makes one note the strong resemblance to A. villosa. The general dimensions of culm, leaf (shape, surfaces, ciliate blade margins, the geniculate "bend," the character of ligule and auricle) and the feathery panicle of pinkish to silvery-white hairy spikelets, all are deceptively similar. However, a closer look reveals a different plant base, namely caespitose but not rhizomatous, the culms often short-decumbent, themselves geniculate at base and with adventitious roots. In the panicle the spikelets, at first appressed-silky-pubescent, later "fuzzy" with elongate spreading trichomes, are superficially similar to Anthenantia, but a closer inspection reveals (a) lateral compression rather than dorsiventral, (b) two glumes, both keeled apically and aristate, and (c) second glume and lower lemma about equal in length with lower half gibbous, the rounded backs prominently pustular-papillose, the hairs liberally interspersed, not in longitudinal rows, the upper half abruptly narrowed to a strongly-laterally compressed, keeled, aristate (in the glume) beak. Finally, while the two florets are similar in composition to Anthenantia (lower floret with a hyaline, 2-keeled palea and tristaminate flower, the upper one typically perfect and navicular) the lemma and palea are chartaceous rather than coriaceous and show a slight lateral compression. The caryopses, while slightly similar, also show bilateral symmetry and an eccentric style base.

Thus, I have the impression that Leptocoryphium, having so many characters in common, could indeed be merged with Anthenantia, an opinion already given by George Bentham. For Melinis, on the other hand, the symmetry of spikelet, the presence of two awned glumes, the disposition of hairs and papillae on the laterally (rather than dorsiventrally) compressed scales or their tips, and the chartaceous, rather than coriaceous, laterally compressed upper floret constitute a significant set of differences and suggest a different evolutionary alliance

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